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# Directional Selectivity

*Norberto M. Grzywacz and David K. Merwine*

## Introduction

Directional selectivity refers to a neuron's ability to produce substantially different responses for stimulus motions of different direction. A directionally selective (DS) cell will fire many spikes in response to object motion in one direction (the preferred direction) while responding weakly, if at all, for motion in the opposite (null) direction. This directional "trigger feature" is often essentially independent of the contrast, contrast polarity, color, shape, or speed of the moving object. Cells displaying directional selectivity are found in the retinas and visual cortices of all the major vertebrate classes. These neurons support a host of visual tasks, ranging from motion perception, image segregation, and deblurring to the control of eye movements. The extraction of direction of motion is so crucial for vision that it is the first motion-related variable encoded in the visual pathway.

It is impossible, however, to determine the direction of a motion using an individual DS neuron. First, because these neurons have relatively small receptive fields, they can only report motion components that are perpendicular to the gradient of illumination. This phenomenon is known as the aperture problem. Second, motions orthogonal to the preferred-null axis will elicit intermediate, ambiguous responses. Moreover, nonmotion parameters, such as contrast, and motion parameters, such as speed, will affect the amplitude of the DS cell's response. However, by comparing over a population of DS cells, the true direction of a motion can be determined. One needs to compare the responses of DS neurons with different preferred directions. Regardless of object contrast or speed, the neuron whose preferred direction is closest to the actual direction of visual motion will have the largest response. Thus, a comparison of responses over a population of DS neurons can disambiguate the veridical motion direction.

### *Optic Flow*

According to physics, the most fundamental variable of motion is velocity, a vector composed of direction and speed. Animals perceive three-dimensional (3D) velocities in the world through the world's two-dimensional (2D) projection onto these animals' retinas. Therefore, the true values of velocity in the world cannot be directly determined using the information from the eyes. A more useful velocity-related variable for the animal is *optic flow*. This is the spatial distribution of velocity vectors that is obtained by projecting the moving 3D world onto the 2D retina. An example of the utility of optic flow analysis occurs when an animal moves forward in a straight line. The resultant optic flow is that of an expansion, and the animal can maintain its heading by keeping the focus of expansion constant (see also MOTION PERCEPTION: NAVIGATION). To find this focus, information about directional selectivity must be combined across the image by "higher" cortical areas. One area that may contribute to this computation is the middle superior temporal cortex (MST), which appears to contain neurons tuned to expansion and contraction (for a review, see Andersen, 1997).

Mathematically, the most popular definition of optic flow uses the image constraint equation $dE/dt = 0$, where $E$ is the brightness of the image (see Grzywacz, Harris, and Amthor, 1994, for details and references). This equation assumes that brightness varies slowly over time and defines the optic flow $\vec{v}$ as

$$\nabla E \cdot \vec{v} + \frac{\partial E}{\partial t} = 0 \qquad (1)$$

This brightness-related definition is not unique, as nonmotion parameters, such as reflectance, can influence the solutions of the equation. Other definitions emphasize different useful components of the motion. For instance, the directional components alone have proved sufficient for determining heading direction as well as for recovering structure from motion and performing image-segregation tasks.

### *Speed*

Before we embark on a detailed discussion of directional selectivity, we would like to comment briefly on the measurement of speed. This variable is considerably more difficult to measure than direction, as a local determination of speed in the image requires precise spatiotemporal information. In contrast, a measure of direction of motion requires two fairly imprecise positional measurements separated in time. For this reason, the visual system computes local speed with relatively less precision than direction and does so at a later stage of processing.

Computational models have been proposed that use DS signals to obtain local speed (reviewed in Grzywacz et al., 1994). For instance, Grzywacz and Yuille developed such a model by using model DS cells with receptive field profiles based on Gabor functions. They organized these cells in a 3D space whose coordinates were the optimal temporal frequency and the two components of optimal spatial frequency of the cells. They found that any arbitrary translation with constant velocity would yield maximal responses that fell on a plane in this space. Local speed and direction could then be determined by measuring the slant and tilt of this plane. Grzywacz and Yuille proposed a plausible neural architecture for performing this measurement.

## Theory of Directional Selectivity

Reichardt, Poggio, and colleagues (Poggio and Reichardt, 1976) described the theoretical requirements for any model of directional selectivity (see also MOTION PERCEPTION, ELEMENTARY MECHANISMS). The first requirement is spatial asymmetry. If a neuron responds better to a motion coming from the left than to a motion coming from the right, then there must be some difference in the inputs from the left and right sides of the cell's receptive field.

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# Dissociations Between Visual Processing Modes

*Bruce Bridgeman*

## Introduction

The visual system has two kinds of jobs to do. One is to support visual cognition or perception—knowledge about the identities and locations of objects and surfaces in the world. Another, sensorimotor, function is to control visually guided behavior. The two functions require different kinds of visual information.

The cognitive function is concerned with pattern recognition and with the positions of objects relative to one another. Executing this function requires extensive interaction between bottom-up image data and top-down information about objects, faces, etc. Qualitative location information may be adequate for this function; humans are poor at quantitatively estimating distances, directions, etc. if the measures of these abilities are perceptual judgments rather than motor behaviors.

The sensorimotor function, in contrast, needs quantitative egocentrically calibrated spatial information to guide motor acts. It does not need the minute-of-arc acuity of the cognitive function, however: calibration is more important than resolution. As a result, the brain's sensorimotor representations can be much smaller than those supporting cognition.

It is an empirical question whether these two functions, the cognitive and the sensorimotor, should be modeled as a single visual representation with two readouts or as separate maps of visual space. There is now extensive evidence for two distinct maps or sets of maps of visual space in the brain, one set handling perception and the other supporting visually guided behavior (Figure 1). Evidence comes from physiological recordings from the separate maps, from neurological patients in which one system or the other is damaged, from fMRI and PET scans of humans doing cognitive or sensorimotor tasks, and from psychophysical work in which different spatial values are inserted into the two systems simultaneously.

Some of the earliest evidence for the two-visual-systems distinction came from experiments in hamsters, where lesions of the midbrain's superior colliculus led to the inability to orient appropriately in a T-maze, combined with preserved abilities in pattern discrimination. In other animals, visual cortex lesions disturbed pattern discrimination without interfering with maze orienting (Schneider, 1969). This forebrain-midbrain distinction changed over the course of evolution, as both spatial orientation and pattern recognition became corticalized in primates.

## Neurophysiology

The visual pathways begin as a unified system, from the retinas through the lateral geniculate nucleus of the thalamus to the primary visual cortex of the occipital lobe. From here, visual signals are relayed to approximately 27 topographic maps in other visual areas (VISUAL SCENE PERCEPTION). This characteristic of visual systems raises a question: do all of these maps work together in a

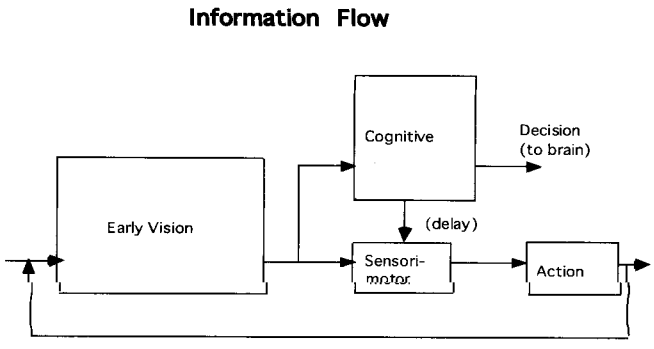


**Figure 1.** Information flow in cognitive and sensorimotor visual pathways. Visual image input is from the left, and cognitive or motor output to the right.

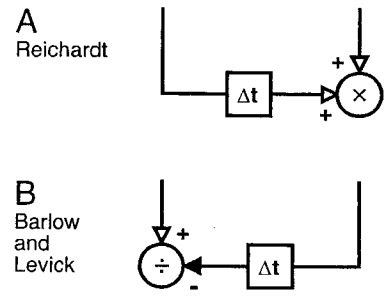


**Figure 1.** Models for directional selectivity. In each case, preferred direction is from left to right. The lines with arrows are inputs to the nonlinear interaction sites (circles). These inputs originate at different spatial locations as indicated by the nonarrow ends of the lines. Boxes with "Δt" symbols indicate that their corresponding lines are slow. Hence, movement going from the slow line to the fast line will generate signals that arrive together at the interaction sites but the opposite movement will not. In the Reichardt model, a multiplication exploits this difference to create directional selectivity. In the Barlow and Levick model, the difference is exploited by an inhibitory (possibly division-like) interaction.

Models for this asymmetry have always included a temporally asymmetric component, that is, some difference in time course between the left- and right-side inputs. However, this need not be the case. For example, the left-side input could "gate" the right-side input (Grzywacz et al., 1994). In this case, the cell will fire only when the motion comes from the left and opens the gate, before reaching the right-side input.

The second requirement for directional selectivity is a nonlinear mechanism. A spatiotemporal asymmetry alone will yield a directional difference in the responses (i.e., differing waveforms, depending on the direction of stimulus motion). However, such an asymmetry alone is not sufficient to produce two different single-number responses for preferred- and null-direction motions, a requirement to decide what the estimated direction of motion is. Poggio and Reichardt's work proves that, without a nonlinear mechanism, any numbers obtained from the waveforms of the responses will be equal for all directions of motion. The nonlinearity can be as simple as a threshold or the gating mechanism mentioned above, but it must be present.

Figure 1*A* illustrates the simplest model proposed by Reichardt and colleagues for the insect's retinal directional selectivity (RDS). For simplicity, the model uses inputs from only two locations. The proposed spatial asymmetry in this model is temporal. Inputs from the preferred side (the side first encountered by an object moving in the preferred direction, left in the figure) are propagated to the interaction site on a slow time scale compared with those from the null side. The proposed nonlinearity for the interaction is a multiplication. Thus, if an object moves in the preferred direction at an appropriate speed, the slowness of the left-side pathway is compensated for by the earlier arrival time of the stimulus, causing both inputs to arrive at the decision site at the same time, yielding a positive multiplication. For null-direction motions, the inputs will arrive at the decision site separately, and the result of the multiplication will be zero. The multiplicative nonlinearity therefore acts as a coincidence detector.

This multiplicative nonlinearity is one of many quadratic nonlinearity models supported by insect data. Poggio and Reichardt used the Volterra series formulation to examine the predictions common to all quadratic models of directional selectivity. For such a formulation of a smooth, time-invariant, nonlinear interaction between the responses to stimuli in spatial locations $a(z_a)$ and $b(z_b)$, the output is

$$y(t) = h_{0,0} + \sum_{m=1}^{\infty} \sum_{j=0}^{m} h_{j,m-j} *^m z_a^{(j)} z_b^{(m-j)} \qquad (2)$$

where $*^m$ is the $m$th-order convolution and where $h_{j,m-j}$ are the $m$th-order kernels of the interaction. The $m$th-order kernel describes the nonlinear interaction between the responses to stimuli at $m$ different instants in time. A quadratic nonlinearity is one for which if $m \geq 3$, $h_{j,m-j} = 0$. A quadratic nonlinearity thus describes multiplicative interactions between pairs of stimulus responses.

Two predictions of quadratic nonlinearity models are frequency doubling and superposition of nonlinearities. Frequency doubling is the appearance in the Fourier spectrum of the response to moving sinusoidal gratings of energy at a frequency of twice the fundamental but not at frequencies higher than that. In superposition of nonlinearities, the average of the nonlinear response to a grating composed of two sinusoidal gratings of different frequencies (whose ratio is a rational number) is equal to the sum of the responses to the two individual gratings. Both frequency doubling and superposition of nonlinearities can be used to test whether a system computes directional selectivity solely through quadratic nonlinearities.

## Retinal Directional Selectivity

Although DS retinal neurons have been described in a number of vertebrates, the vast majority of work has been performed in the rabbit. In this animal, two types of DS cells have been described. The first, the On-Off DS ganglion cell, responds well to moving spots, bars, edges, or gratings of both contrast polarities over a broad range of speeds. Additionally, these cells can detect the direction of motion of long edges for displacements less than the spacing between photoreceptors, hence mediating directional hyperacuity. Four subtypes of On-Off DS cell exist, one each for temporal, nasal, superior, and inferior motions. Each subtype independently tiles the retinal surface and thus can independently sample the visual world. The second DS cell type (the On DS cell) responds only to bright edges and to considerably slower speeds than those preferred by the On-Off type. The On DS cells exist in three subtypes whose preferred directions are aligned with the animal's semicircular canals. These cells have receptive fields whose areas are more than three times larger at any given eccentricity than the On-Off type, and their tiling is correspondingly less dense (Vaney et al., 2001). The On DS type supports optokinetic nystagmus through projections to subcortical areas. As they are infrequently encountered, the mechanisms responsible for these cells' directional selectivity have not been well investigated, and they will not be considered further here.

### *Spatial Asymmetry*

Although a spatial asymmetry is required for generating a DS circuit, no obvious asymmetry exists in the anatomical structure of the On-Off DS cell. The dendritic trees of these ganglion cells have a unique, looping morphology. But there is no relationship between asymmetries in the tree and the cell's preferred direction of motion (Vaney et al., 2001). Therefore, the spatial asymmetry has been conjectured to exist in the connectivity between DS cells and their inputs. No spatially asymmetric connections have been conclusively identified to date. However, two strong candidates exist. First, cross-correlational and anatomical studies of the cholinergic amacrine cell and the On-Off DS cell suggest that the former makes spatially asymmetric connections to the latter. Support for this suggestion comes from the elimination of DS responses to moving gratings by cholinergic antagonists (Grzywacz, Amthor, and Mer-

wine, 1998). Second, asymmetric connections may also exist from some GABAergic amacrine cells to the DS cells. GABA antagonists strongly reduce directional selectivity.

### *Nonlinearities*

In their seminal work on rabbit retinas, Barlow and Levick (1965) performed two-slit apparent-motion experiments on DS cells. They discovered that when two stimuli were presented in null sequence (as if an object were moving in the null direction), then the number of spikes elicited was far less than the sum of the spikes for each stimulus in isolation. From this, they concluded that RDS arises from a nonlinear, *inhibitory* mechanism that "vetoes" responses to null sequences (equivalent to the logical AND-NOT operation). As shown in Figure 1*B*, their proposed spatial asymmetry has two components. A central component is excitatory and is conducted to the interaction site quickly. A second, inhibitory component is offset to the null side and is conducted with a delay. Thus, an asymmetry exists in both the sign and time course of the two spatially separated components. This asymmetry causes motions in the preferred direction to yield responses, while responses to null-direction motions are vetoed. However, despite Barlow and Levick's proposal, this veto mechanism turns out not to be a perfect veto. Studies reviewed by Grzywacz et al. (1994) show that a better description for the inhibitory interaction is a division-like nonlinearity, as shown in Figure 1*B*.

Torre and Poggio proposed a biophysical implementation of Barlow and Levick's inhibition (see Grzywacz et al., 1994, for a review). Because RDS can be elicited by motions spanning remarkably short distances almost anywhere within the DS cell's receptive field (Barlow and Levick, 1965), Torre and Poggio suggested that the inhibition acted separately within each branch of the cell's dendritic tree. To constrain the computation spatially, they suggested that the inhibition works through a synapse that causes local changes of membrane conductance (shunting inhibition) and little hyperpolarization. To understand such a synapse, consider a patch of membrane receiving excitatory ($g_e$) and shunting inhibitory ($g_i$) synaptic conductances. Setting without loss of generality the resting and inhibitory reversal potentials to zero, the voltage $V$ obeys

$$C\frac{dV(t)}{dt} + (g_e(t) + g_i(t) + g_{\text{leak}})V(t) = g_e(t)E_e + g_{\text{leak}}E_{\text{leak}} \tag{3}$$

where $C$ is membrane capacitance, $g_{\text{leak}}$ is the membrane's leak conductance, and $E_e$ and $E_{\text{leak}}$ are reversal potentials of $g_e$ and $g_{\text{leak}}$, respectively. When $g_i \gg g_e$, then $V$ falls toward the following equilibrium value:

$$V(t) \rightarrow \frac{g_e E_e + g_{\text{leak}}E_{\text{leak}}}{g_i} \tag{4}$$

which is small, because $g_i$ is large. Therefore, this inhibition is division-like rather than subtraction-like. Torre and Poggio argued that a shunting-inhibition mechanism might also be consistent with the insect's quadratic nonlinearity, because, for sufficiently low contrasts, one can ignore the higher-order nonlinearities, as in a Taylor series approximation. However, experimentally a quadratic approximation is not valid for rabbit DS cells, as they fail both the frequency-doubling and superposition-of-nonlinearities tests even at near-threshold contrasts.

Although a shunting-inhibition mechanism can theoretically produce the localized interactions necessary to explain many DS properties, it has not been possible to record intracellularly within dendrites to test this mechanism. Recently, two additional nonlinearities have been proposed that could support dendritically localized directional selectivity. First, it has been suggested that this nonlinearity could be due to excitatory voltage-dependent conductances at the dendrites. There is evidence of dendritic spikes in rabbit's ganglion cells. Second, it has been proposed that the unusual predominance of NMDA glutamatergic receptors on DS cells may have functional significance. The NMDA channel has a nonlinear behavior, due to channel blockade by magnesium ions at hyperpolarized potentials. Therefore, glutamatergic binding must occur *during depolarization* for the channel to operate. Even weak, null-direction inhibition could cause the NMDA channel to hyperpolarize and close. It could therefore act as the veto site hypothesized by Barlow and Levick (1965). When tested in magnesium-free medium, RDS is severely reduced, suggesting a critical role for NMDA receptors. The NMDA, spiking, and shunting nonlinearities need not be mutually exclusive, and each could play an important role in supporting robust RDS.

### *Pre- or Postsynaptic Nonlinearities?*

In addition to the null-direction inhibition just described, it is known that preferred-direction motions facilitate DS cell responses (Barlow and Levick, 1965). If the spatiotemporal parameters of the stimulus are appropriate, then preferred-direction facilitation can be as strong as null-direction inhibition (reviewed in Grzywacz et al., 1994). Facilitation is believed to come to the DS cell from the cholinergic amacrine cells. A spatial asymmetry has been shown to exist in the input-output relationship of these cells' dendrites. These dendrites receive excitatory inputs along their length, but they release excitatory transmitter (ACh) and may receive inhibitory inputs (through GABA) only at their tips (Figure 2*A*). If the GABA-inhibition acts in a division-like manner, then each dendrite contains a spatial asymmetry and a nonlinearity, and thus can act as an autonomous DS unit. Hence, it has been proposed that DS signals are at least partially generated presynaptically and flow from the cholinergic dendrites to the DS cell. DS cells would then

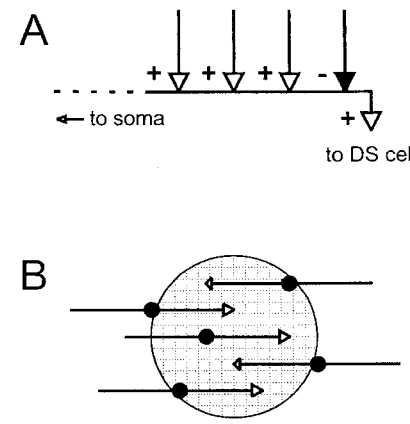


**Figure 2.** Schemes for presynaptic retinal directional selectivity. *A*, Model of a cholinergic-dendritic DS subunit. The bent line represents a dendrite of the cholinergic amacrine cell making a synapse onto a DS cell. This dendrite receives excitatory inputs throughout its length (open arrows) and inhibitory inputs (filled arrow) near the synaptic ending. Therefore, the output synapse is directionally selective, as the dendrite behaves like a Barlow-and-Levick model (Figure 1*B*). *B*, Spatial relationship between cholinergic dendrites and the DS cell's receptive field (circle). Arrowhead size indicates synaptic strength, and black discs mark the cholinergic somas. Although all dendrites are directionally selective, the DS cell receives more inputs from the left than from the right. Consequently, its preferred direction is to the right.

preferentially sample from dendrites with the same preferred direction (Figure 2*B*).

There is accumulating evidence, however, that both pre- and postsynaptic asymmetries may be involved in RDS. Complete blockade of cholinergic synapses does not fully eliminate RDS to moving bars (Grzywacz et al., 1998). The residual direction selectivity is GABAergic and appears to be postsynaptic. In turn, GABA blockade not only does not always eliminate RDS, it occasionally reverses its preferred and null directions. Computer simulations of the cholinergic-dendritic RDS can account for these reversals as a result of synaptic saturation (reviewed in Grzywacz et al., 1994). Thus, asymmetric postsynaptic inhibition and asymmetric presynaptic facilitation may act cooperatively to produce robust RDS for a broad range of visual stimuli.

### *Development*

The development of RDS is not well understood. In turtles, RDS emerges late in development, that is, after the establishment of concentric receptive fields, inhibitory surrounds, and orientation selectivity (selectivity to spatial orientation of anisotropic stimuli, such as lines) (Sernagor and Grzywacz, 1995). Evidence suggests that turtle RDS may emerge at the expense of orientationally selective (OS) cells. It has thus been proposed that turtle DS cells are modified OS cells. This late emergence of RDS suggests two hypotheses for its development: (1) it requires light exposure, and/or (2) it requires the late emergence of an inhibitory drive onto the network mediating orientation selectivity.

In rabbits, however, RDS emerges relatively early. The percentage of DS cells and DS cell gap-junctional coupling patterns both appear adult-like within a few days of eye opening. Directionally selective responses have been recorded from rabbit retinas before eye opening. Therefore, some authors have suggested that rabbit RDS is initially generated in the presynaptic cholinergic circuit. The primary excitatory stimulus for this mechanism would be the bursting spontaneous waves of activity known to occur during development (see Sernagor and Grzywacz, 1995, for references on developmental spontaneous activity). In this case, the first challenge for the DS cells would be to connect selectively to cholinergic dendrites of similar orientation. (Recall that the amacrine cell dendrites can each act as a DS subunit.) A Hebbian correlational process that would reinforce statistical biases in the initial contacts from the cholinergic dendrites to proto-DS cells could produce this selectivity. GABAergic null-direction inhibition would then be added to the cell's established directional preference.

## Cortical Directional Selectivity

DS cells are found in multiple locations in the cortices of mammals, beginning with simple DS cells in the lateral geniculate nucleus (LGN) input layers of the primary visual cortex (V1). Nearly every simple and complex cell in mammalian V1 has some degree of directional selectivity. However, the strength of directionality varies widely. For example, only about 20% of macaque V1 DS cells achieve preferred-versus-null response ratios greater than 3:1 (De Valois et al., 2000). In comparison, rabbit retinal DS cells typically have preferred-null ratios around 10:1. As with the retinal DS cells, the preferred direction of motion cannot be accounted for by any spatial asymmetries in the dendritic trees of the cortical DS cells. However, unlike retinal DS cells, cortical DS cells are highly selective for the orientation and spatial frequency of the moving stimulus. Moreover, it is often possible to predict the preferred direction of motion for a simple DS cell from its spot-mapped receptive field. This has led to the development of quasilinear models of cortical directional selectivity, which we discuss below.

There is abundant evidence that cortical directional selectivity supports motion perception. Perceptual decisions in motion tasks correlate with the performance of cortical DS neurons (Andersen, 1997). Furthermore, lesions and/or current injections in MT affect motion integration tasks, biasing motion perception in specific and replicable ways (Salzman et al., 1992). In addition to the contribution of cortical DS cells to perception, they probably also assist in the control of eye movements. For instance, neuroanatomical data demonstrate that both MT and MST send large projections to the dorsolateral pons, an area known to be involved in smooth-pursuit eye movements.

### *Hierarchy*

As a first-order approximation, motion is computed hierarchically in the cortex (Andersen, 1997). The hierarchy begins with the simple and complex DS cells in layers IV and VI of cortical area V1, as just described. (In animals phylogenetically close to primates, retinal DS cells project primarily to subcortical centers. Evidence suggests that directional selectivity in the primary visual cortex is computed independently from RDS.) The DS cells in V1 project to the MT cortical area (MT or V5) and to V2, which also projects to MT. Directional selectivity becomes more complex in MT; that is, cells there typically have very large, orientation-independent receptive fields, and many will respond best to the composite motion of a plaid, as opposed to its individual components. From MT, the motion pathway projects to MST, wherein directional selectivity information is further combined to produce neurons sensitive to complex motions, such as rotation, expansion, and contraction (Andersen, 1997).

### *Psychophysical Models*

One class of models for the first stage of cortical directional selectivity is based on human psychophysics and is similar to the Reichardt model in Figure 1*A*. In these models a slow, laterally displaced input and a fast central input are multiplied. As described above, the two signals from these inputs will arrive simultaneously, yielding a response, for only one direction of object motion. Another class, called motion-energy models (Adelson and Bergen, 1985), proposes a distributed spatiotemporal asymmetry and a squaring nonlinearity (Figure 3*A*). The distributed spatial asymmetry occurs because different locations in the receptive field have different impulse responses. This property is known as space-time (S-T) inseparability and is illustrated in Figure 3*B*. For this type of space-time arrangement, it is only for preferred-direction motions that the responses of all areas occur simultaneously. Simple linear summation then results in differential responses to preferred- and null-direction motions, and the squaring nonlinearity converts this directional difference into directional selectivity.

### *Physiological Models*

There is substantial physiological evidence for S-T inseparability in simple DS cells in visual cortex. Figure 3*C* shows an idealized simple-cell receptive field map as would be obtained from reverse-correlation experiments (De Valois et al., 2000). The cell contains on and off subregions with different time courses in different portions of space, resulting in an oriented spatiotemporal receptive field. Assorted variations of linear energy-motion models with static nonlinearities have been proposed that can account for approximately 50%–80% of the response of simple DS cells (Reid, Soodak, and Shapley, 1991; De Valois et al., 2000). However, the correlation between simple-cell S-T profile and direction selectivity varies widely in V1. Cells in layer IVB show very high correlation, those in IVA show only moderate correlation, and those in layer

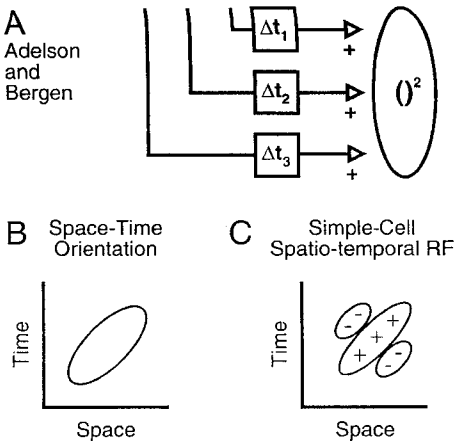


**Figure 3.** Motion-energy models of cortical directional selectivity. *A*, The Adelson and Bergen model. The symbols here are as in Figure 1, with "( )$^2$" indicating a squaring operation. *B*, Space-time orientation. If in *A*, $\Delta t_3 < \Delta t_2 < \Delta t_1$, then a plot of the response of the model to stimulation at different positions in space looks like this figure; that is, it is oriented in space-time. Hence, a motion going from left to right will have a positive slope in this plot and cause much response, whereas the opposite motion will not. *C*, Idealized representation of a simple-cell receptive field. The inhibitory flanks help to inhibit motions in the null (nonpreferred) direction (lines with negative slopes).

VI show very low correlation, despite equivalent directional tuning (Murthy et al., 1998). Thus, S-T structure alone cannot fully account for simple DS cell responses. In addition, quasilinear models of simple cells generally overestimate nonpreferred responses and sometimes underestimate preferred responses (Reid et al., 1991). And linear feedforward models also do not predict onset transients, which are commonly observed. Therefore, inhibitory (Reid et al., 1991; Heeger, 1993) or excitatory (Douglas and Martin, 1992) nonlinear feedback interactions between cortical cells have been proposed to account for these discrepancies. It has also been suggested that nonpreferred direction suppression might be due to a cortical inhibitory network devoted to response normalization (Heeger, 1993).

Although it has been accepted for many years that magnocellular cells from the LGN provide the input to the motion system, motion-energy models require inputs to simple DS cells that differ in latency (or temporal phase). Magno cells all have essentially identical response timings and therefore could not provide the range of latencies needed without an intracortical mechanism for creating delays (De Valois et al., 2000). It has been shown that blockade of cortical $GABA_A$ inhibition reduces but does not eliminate S-T inseparability. Thus, intracortical inhibition may contribute to, but cannot be solely responsible for, input latency differences. Humphrey, Saul, and Fiedler (1998) note that about 40% of parvocellular geniculate cells display absolute phase delays and long latencies (lagged cells) relative to the remaining parvo cells (nonlagged cells). Because lagged and nonlagged timing signatures are identifiable in simple-cell receptive fields, these authors attribute S-T inseparability to converging lagged and nonlagged parvo cell inputs with spatially shifted receptive fields. De Valois et al. (2000), however, suggest that the requisite latency differences arise from two classes of nondirectional (preferred-null ratios <3:1) cortical cells, which receive inputs from magno and parvo cells. Both nondirectional types can be found in a single cortical column and have appropriate differences in response waveforms. Additionally, these two nondirectional cell types are often shifted 90° in spatial phase, though centered on the same spatial location. Thus, they have exactly the spatiotemporal profile required to detect direction of motion using a linear energy-motion model.

Complex DS cells are generally found in the upper and lower layers of V1. Unlike most simple DS cells, complex DS cells lack first-order (linear) S-T oriented receptive fields. However, these cells show second-order (quadratic) S-T structure. In other words, it is the interactions between two sequentially stimulated locations in the cell's receptive field that are S-T inseparable. Thus, dynamic nonlinearities have been proposed to account for complex-cell directional selectivity. These nonlinearities would facilitate or inhibit, respectively, the responses to preferred- or null-direction motions. Similarly, S-T separable simple cells have also been shown to display some second-order, that is, nonlinear S-T structure. Because there is evidence for complex-to-simple-cell interactions, it has been proposed that directional selectivity and second-order S-T inseparability in simple cells arise from complex-cell inputs.

### *Development*

At least 5% of the cells in areas V1 and V2 of the kitten are directionally selective at eye opening. Thus, some of the cortical directional selectivity is either genetically coded or epigenetically derived through developmental spontaneous activity. Interestingly, selective biases in the distribution of preferred directions can be produced in kittens by exposing them to stripes moving in a particular direction after eye opening. In addition, one can nearly eliminate cortical directional selectivity by raising animals in an environment that is illuminated only by brief, low-frequency, stroboscopic flashes of light. Under these rearing conditions, only about 10% of V1 cells develop directional selectivity, and their directional selectivity is considerably weaker than normal. Not surprisingly, elimination of S-T inseparability accompanies the loss of directional selectivity (Humphrey et al., 1998). Perceptually, strobe-reared cats require contrasts at least ten times higher than normal to determine the direction of a moving grating. Furthermore, these elevations in contrast threshold can be permanent. No recovery of S-T structure or improvement in contrast threshold was found in two cats that had received 12 years of training following strobe rearing. Thus, it appears that some critical period exists during development during which directional selectivity must be established or it is forever compromised.

Based on the loss of S-T inseparability during strobe rearing, some authors have modeled the development of cortical directional selectivity as due to inputs with different response timings forming connections with a common cortical cell. These connections would self-organize through a Hebbian process that would strengthen the synaptic connections of well-correlated inputs (Humphrey et al., 1998). Strobe rearing would restrict the range of timings that could be associated, and therefore could eliminate cortical directional selectivity.

## Discussion

In this article, we have discussed the first step in the perception of motion—the determination of motion direction. This information is encoded by ensembles of directionally selective neurons both in the retina and within multiple visuocortical nuclei. Elucidating the cellular mechanisms subserving directional selectivity has been a major goal of neurobiologists for nearly 40 years.

**Road Map:** Vision
**Related Reading:** Feature Analysis; Motion Perception: Elementary Mechanisms; Retina; Visual Cortex: Anatomical Structure and Models of Function